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SECOND ARTICLE.

By CHARLES SEDGWICK MINOT,

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Concerning the majority of invertebrates, we have a very imperfect knowledge in respect of their auditory apparatus. The molluscs are the only class the otocysts of which have been sufficiently studied to enable us to give a comparative treatment. It is greatly to be desired that investigations, similar to those of the Brothers Hertwig on medusæ, should be carried out upon the higher radiates and the vermes. The following pages illustrate the extreme necessity of such investigations.

2. The Ctenophoræ.

The Ctenophoræ all have eight meridional rows of cilia. The *Cestum veneris* was formerly erroneously supposed to have four only, a mistake due to the rudimentary condition of four of the rows. Toward the aboral apex of the animal the eight rows unite to form four, which run toward the centre of the apex, each ending in a plate of cilia. Between the four plates is a bundle of concrements, forming a mulberry-like sphere. This sphere is covered over by a dome, the origin and morphology of which is not understood. The ectoderm around the apex forms an area of

modified cells, including four groups of pigmented cells, containing each a refractile body, quite different from the concrements in the centre. Around this area are four *polar plates* of ciliated cells.

This apex has generally been regarded as the nervous and sensory centre of the animal, and the central sphere of concrements as a mass of otoliths. The last-mentioned structures were first noticed by Milne-Edwards,[1] and later by L. Agassiz,[2] who both considered them eye-specks, which they certainly are not. Since then they have been mentioned by many authors, some of whom have added a little, but not much, to our knowledge of them. Recently two extensive memoirs upon the nervous system of Ctenophoræ have appeared. The first, by Eimer,[3] describes a complicated set of ganglion-cells and nerve-fibres scattered through the body, nowhere gathered into a ganglion, and having no special relation to the otoliths. The second, by Chun,[4] who found no nervous system at all, and denies the correctness of Eimer's statements. He advances, however, the very queer opinion that the ciliated bands are the nervous system, solely on the ground that when a beat of the cilia is started at the apex against the sphere of concrements, it runs wave-like centrifugally along the band! Such a view, of course, cannot for a moment be seriously entertained, because a wave-like propagation of the beat is a general characteristic of ciliated surfaces, and certainly is no index of a nervous system. Chun failed to find any nervous elements, or, what is of especial interest to us, any sensory cells in the neighborhood of the concrements. From this review it is evident that we cannot assert that the concrements are part of an auditory appara-

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[1] Edwards, H. Milne: Observations sur la Structure et Fonctions de quelques Zoophytes, Mollusques et Crustacés des Côtes de la France. Ann. Sci. Nat., XVI. (1841), 193–232 (*Vide* pp. 205–206).

[2] Agassiz, Louis: Contributions to the Natural History of N. A. Acalephæ. Pt. II., Mem. Am. Acad., IV. (1850), 313–374 (*Vide* Pl. V., figs. 9, 10).

[3] Eimer, Th.: Zoologische Studien auf Capri (I. Ueber *Beræ ovatus*, pp. 52–82).

[4] Chun, Carl: Das Nervensystem und die Muskulatur der Rippenquallen. Abh. Lenkberg. Natforsch. Ges., XI. (1878), 181–232, 2 Tafeln.

tus. At most, we can only say that, according to the observations of Kowalewski,[1] confirmed by Chun, the concrements are developed like true otoliths in the interior of cells of the ectoderm, afterward falling out to be added by the action of the surrounding cilia to the sphere. I cannot but think Chun's account of the apical region not entirely accurate. Indeed, the Brothers Hertwig, in their paper[2] on "Actinien," incidentally contradict his views, as does also Hartmann,[3] so that we may safely consider his singular hypothesis in regard to the nervous system and the function of the concrements to have been definitely set aside.

To conclude, we cannot tell whether the Ctenophores have an auditory organ or not.

3. The Echinoderms.

Our knowledge of the organs of hearing of this class is confined to a single observation, of somewhat problematical character, upon *Synapta digitata*, by Baur.[4] He found five pairs of closed vesicles upon the radial nerves, close to the oral calcareous ring. Each vesicle is united with the neighboring nerve by a short pedicle. The vesicles are lined by an epithelium resting upon a fibrous *tunica propria.* They have, at the time when the Synapta has just completed its metamorphosis, one or several bodies in their interior, which are round, quite homogeneous, highly refractile, and constantly trembling, but in the fully grown animal they were not found. Johannes Müller observed them in the young Synapta. As these vesicles contain concrements, they are possibly auditory sacs with otoliths. This possibility is the whole of our knowledge of the organ of hearing in echinoderms.

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[1] Kowalewski, Anton: Entwickelungsgeschichte der Rippenquallen. Mém. Acad. St. Petersb. X., (1866), 4me Mém.

[2] Hertwig, O. and R.: Jena Zeitschr. Natwiss., XIII. 1879.

[3] Hartmann: Einige Verhältnisse in der Organisation von Pleurobrachia pileus. Sitzber. Natforsch. Ges. Berlin, 18 Febr., 1879.

[4] Baur, Albert: Beiträge zur Naturgeschichte der Synapta digitata. Erste Abh., S. 46-47. Nova Acta L—C. Akad. XXI. 1864.

4. The Mollusca.

Since the best researches assign to the rotifera and brachiopoda immediate relationship with the molluscs, it would be proper to describe their otocysts next; but, unfortunately, we can only say that in certain forms of both the classes above-named a vesicle or pair of vesicles have been observed, which a vague surmise has interpreted as otocysts.

In the true mollusca there are normally a pair of otocysts, which arise, and usually permanently remain, near the pedal ganglion, although the auditory nerve has its origin in the brain or supra-œsophageal ganglion. Formerly the otocysts of Lamellibranchs were supposed to be innervated from the pedal ganglion; but Simroth[1] has shown that the nerve descends with the commissure part way to the vesicle, or, in other words, that the nerve appears to arise from the œsophageal ring.

The otocysts were first observed in the Cephalopods by John Hunter;[2] in the Heteropods and Pteropods, by Eydoux et Souleyet,[3] in 1838, followed the next year by independent and more accurate investigations by Krohn;[4] in the Lamellibranchiata, by Siebold,[5] in 1838; in the Gasteropoda, by Siebold,[6] in 1841. Since then a considerable number of authors have contributed to our knowledge of these organs. A list of the more important papers is given on p. 261, and the works themselves are referred to in the following pages by the Roman numerals prefixed to the titles on that list. It is to M. Lacaze-Duthiers that we are indebted for the very acceptable name *otocyst*.

Concerning the very first development of the auditory vesicle,

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[1] Simroth: Zeitschr. f. wiss. Zool., XXV., pp. 269, 270. 1875–76.

[2] Hunter's Works, Vol. IV., p. 294. Reprinted from Phil. Trans., p. 379. 1782.

[3] Eydoux et Souleyet: L'Institut, 1838, No. 255, p. 376 (Transl. Wiegmann's Arch., 1839, II., 215, and Froriep's N. Not., Nro. 175, p. 312).

[4] Krohn: Müller's Arch., 335. 1839.

[5] Von Siebold: Müller's Arch., p. 52. 1838.

[6] Siebold, C. Th. von: Ueber das Gehörorgan der Mollusken. Wiegmann's Arch., I., 148–166, Taf. VI. (This is by far the most important of all the earlier memoirs.)

the observations are not numerous; but in a few species there is a small invagination of the ectoderm on the side of the foot, not far from the pedal ganglion, and immediately behind the primitive kidney (*Urniere*), when that structure is present. For example, in *Fusus* it has been observed by Bobretzky (I., p. 133, Taf. XII., figs. 80, 81); in *Firiloides* by H. Fol (IX., pp. 134, 135, Pl. II., fig. 28, *wi.*); and in *Loligo* by Brooks (III., p. 9, fig. 9, *er.*). The invagination is afterward constricted around the neck, and so soon becomes converted into a closed vesicle. The cells which form the otocyst are thicker and larger than those which remain to form the epidermis. The differentiation of our organs begins very early, about the same time as the eyes, and before the histological differentiation of the nervous system. Gegenbaur, however, states that the ear first appears in Limax as a solid group of cells (XII., p. 385), which afterward becomes hollowed out. There can hardly be much doubt that this opinion is based upon an imperfect observation. Application of the general principles of embryological specializations justifies the provisional assumption that the otocysts are developed in all molluscs as a pair of ectodermal invaginations. A layer of mesoderm early appears around the young otocyst, and forms ultimately the *tunica propria*, upon which the epithelium rests. The otoliths arise later in the epithelium (Fol), and gradually enlarge. They are, therefore, cellular concrements. So long as the first appearance of these deposits were unknown, the opinion prevailed that they were formed by precipitation in the fluid of the vesicle. This view was always without much plausibility, because all morphological elements are, so far as known, always formed by the direct action of cells, the nearest approach to an exception being the deposit of substances in cell-walls, as, for instance, in the formation of shells. Shortly after the otoliths are formed, cilia appear in the interior of the auditive vesicle, and impart (?) a constant trembling motion to the ear-stones. Apparently the vesicle is filled with fluid from the very first; but thereabout is much uncertainty.

The primitive form of the vesicle is approximately spherical, since this is its shape in all young molluscs. Its primitive size is so small that its epithelial wall consists of only a few, or at most a small number of shells, about as high as they are broad.

There is a single small spheroidal otolith, which in *one type* of ear remains single, but in that case enlarges greatly—sometimes enormously, while its shape remains nearly the same. In the second type, the otolith remains small, growing a little and generally changing its form, and a considerable number of otoliths are added, duplicating the first many times. The Lamellibranchs, *Dentalium*, and most Gasteropods have an ear preserving tolerably these original types. In the Heteropods we find a very great enlargement, and other specializations of a histological character, of which later. Finally, in the Cephalopods, in addition to the large size, occur modifications of shape (Owsjannikow und Kowalewski, XX., pp. 17, 18).

In certain Gasteropods (cf. Lacaze-Duthiers, XV.) there is a tubular prolongation of the vesicle embraced by the nerve. Boll (II., 75) from his observations thinks it possible that this canal may be present in all Gasteropoda. In the dibranchiate Cephalopods there is a similar canal, which was first observed by Kölliker, and has been named the *Ductus Kollikeri* by Grenacher; the duct is the remnant of the tube, which, for a time, connects the vesicle with the orifice of the primitive invagination. Its embryological significance was first indicated by Ray Lankester, and definitely proven by Grenacher. In the Octopoda the otocyst does not otherwise vary greatly from the simple spheroidal form; but in the Decapoda, Owsjannikow and Kowalewski (XX., 17, 18), basing their observations upon *Sepia officinalis*, found several projections[1] from the wall into the interior of the vesicle, and large enough to be visible to the naked eye; also several recesses. Neither the protuberances nor cavities bear the sensory cells, and their functional value cannot be guessed. In the tetrabranchiate cephalopods (*Nautilus*), on the other hand, in agreement with the lower rank of the animal, the ear has a simpler form, being merely a rounded sac, lying near the eye.

The primitive position is at the side of the foot; but in many species the otocysts, after they have been formed, change their places.

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[1] O. and K. have given the glaringly inappropriate name of *ampullæ* (! !) to these projections.

Very frequently they move toward the median ventral line, and may even travel so far as to meet on the median line right below the pedal ganglion. This occurs in the Cephalopoda, in which the two otocysts are separated only by a thin partition. Again, in many Gasteropods, they pass forward to a position behind the eyes (certain Heteropoda and Apneusta), or even come to lie against the supra-œsophageal ganglion itself (*e.g.*, Doris, Æolis, Tergipes, etc.). Morphologically, the original proximity to the pedal ganglion has a peculiar and very profound significance, first recognized by Hatschek.

Passing now to the consideration of the minute anatomy, we begin with the part derived from the middle germ layer, that is to say, the *tunica propria.*

The outer layer of the vesicular wall is composed of cellular and fibrous elements, and is pierced by the auditory nerve, and, at least, sometimes is thicker opposite to than in the neighborhood of the nervous passage, but is always a thin layer. The cells have been recognized chiefly by their elongated nuclei, but in a few cases they have been seen as typical amœboid connective corpuscles. Outside follows the ordinary connective tissue of molluscs (*zellig-blasiges Gewebe*), except that the calcareous corpuscles are lacking around the vesicle. In the Naiadæ there is a third envelope of a peculiar erectile tissue (Simroth, XXVII., 271), which separates the true *propria* from the surrounding unmodified tissue.

In the *Cephalopoda* the *propria* is very thin, being encased by a capsule formed in the head-cartilage. The cartilage presents the appearance characteristic in this class of animals—the cells having ramified bodies lying in clusters, and possessing one or several, often three nuclei. The proper tunic itself consists of merely a few fibres and remains of cells (Boll, II., 84), and contains an abundant, but fine net of capillaries. At one point it is thickened, forming a prominence which is termed the *Bindegewebswulst*, and consists principally of closely crowded, star-shaped, anastomosing connective corpuscles. The *Wulst* is covered by a flat epithelium like that of the otocyst-wall.

There can be little question that the primitive form of the

epithelium of the otocyst is a layer of large cubical cells, not very numerous, all essentially alike, and bearing very short cilia, which are frequently described as vibratile; to their action the majority of writers attribute the constant oscillation of the otoliths. That the cilia are vibratile I consider more than doubtful, and for the joggling of the small otoliths I prefer to adopt the explanation advanced by von Siebold, and which has since been generally overlooked. Siebold (XXVI., 155, 156) wrote: "Noch besser glaube ich das eigenthümliche Oscilliren der Gehörsteinchen mit folgendem Phänomene vergleichen zu können. Bringt man ein Häufchen groben Sand mit einem Tropfen-Wasser auf den einen Ast einer Stimmgabel und erschüttert man die letztere durch einen mässigen Schlag, so wird man die in dem Wassertropfen zerstreuten Sandkörner sich sogleich im Mittelpunkte des Tropfens sich vereinigen sehen, die einzelnen Körner wühlen und drängen sich unter oscillirender Bewegungen nach dem Centrum des Sandhäufchens, wobei die äusseren Körner von Haufen abgestossen und schnell wieder angezogen werden."

Accordingly, we may safely assume that the otolithic movements are the direct effects of sound-waves.

To return to the lining epithelium, the primitive form is preserved in many Lamellibranchs and in some Gasteropods and Pteropods (Fig. 7).

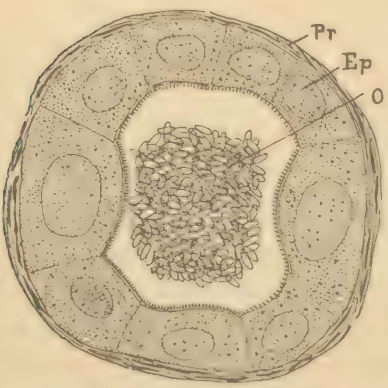

Fig. 7.—Otocyst of Suocinea amphibia, in optical section. after Boll: *Pr*, tunica propria: *Ep*. lining epithelium; *O*, otoliths.

Thus, in *Succinea* and several *Opisthobranchs* the cells are colossal, with a large oval nucleus in their centre. A peculiar modification appears in *Cyclas* (Simroth, XXVII., 274, 275), but Simroth's description and figures do not go very well together, nor do his figures agree with one another. There are large cells with a comparatively small nucleus and a bunch of long bristles; these cells are, perhaps, separated by intervening small cells; in this case there

is a resemblance with Heteropods (*vide infra*). The first modification of the epithelium we have to notice is that the cells are smaller, more numerous, and distinctly cubical or cylindrical in shape (Fig. 8). In the *Naiadæ*, *Neritina* and other Gasteropods, in *Dentalium* and in *Nautilus*, there is such an epithelium, presenting, so far as known, no differentiation of a *macula acustica*. We cannot even guess at the actual succession of these changes either in the phylogenetic or individual development, since each modification in the size and form of the cells reoccurs as we skip from one class to another, and embryologists have failed to note the succession of the alterations in the otic epithelium.

Fig. 8.—Auditory epithelium from the otocyst of Neritina fluiratilis, after Boll.

On the other hand, there is an unmistakable advance in the specialization of the ear in Heteropods and the dibranchiate Cephalopods.[1] In the former class the otocysts present a series of striking peculiarities, which have been very accurately elucidated, as naturalists have always shown a predilection for the study of these organs. The acoustic sac is spherical and encloses a large spherical otolith, Fig. 10, 1; the nerve enters at one side, its fibres radiating over the otocyst; opposite to the nerve is the large *macula acustica*, formed by a thick sensory epithelium; the remaining and larger part of the vesicle is lined by a low epithelium, consisting of two very different kinds of cells: one small and numerous and indifferent, the other larger, bulging above the small cells and bearing a bundle of long bristles. A surface view of this part is shown in Fig. 9. The bristle-cells are star-shaped, giving off five or six tapering processes that end without entering into connection with other parts, and receiving each a nerve-fibre (Fig. 9, A).

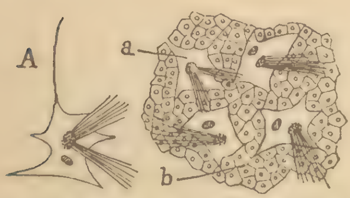

Fig. 9.—Epithelium of the otocyst of Pterotrachea mutica, after Boll: *A* and *a*, bristle-cells; *b*, indifferent cells.

[1] I think it quite possible that closer observation will reveal a *macula acustica* in *Nautilus*, the otocysts of which are very imperfectly known. (Cf. MacDonald, Phil. Trans., 1855, p. 277.)

The protoplasm of these cells is pale, finely granular, and encloses an oval nucleus with several nucleoli. Near the nucleus there is always found a round, dark, granular mass, the *bolster*, from which arises the bundle of bristles. In *Carinaria* and *Pterotrachea coronata* there are some twenty-four, in *Pterotrachea mutica* about fifteen, of these bristle-bearing cells. When at rest the bundles of stiff hairs or bristles recline against the wall of the vesicle, but in the living animals the bundles are suddenly erected after a few seconds' repose; they then stand straight out from the wall, pressing against the otolith. The hairs remain stiff and straight all the time, and must be moved by the action of the cell-body in which they are rooted. The erection lasts two or three seconds, and then the reclining attitude is suddenly resumed (Boll, II., 78, 79). The function of these hairs, and the meaning of their strange jerkings is undetermined, although Boll surmises that the bristle-cells are sensory. It seems equally possible that the nerve of the cell is motor. The *macula acustica* centres around the distal pole, and occupies about one-sixth of the vesicle. It is composed of a central cell, four supporting-cells, and several concentric rows of hearing-cells (Fig. 10 : 1). The hearing-cells have spaces between them, but no one has yet discovered how these spaces are occupied. I anticipate that they will be found to be filled by indifferent cylinder-cells separating the auditory cells, as in Octopus and Sepia (see below). The central cell is 30μ high and about the same in diameter; it produces a slight bulging of the outer membrane; on the central

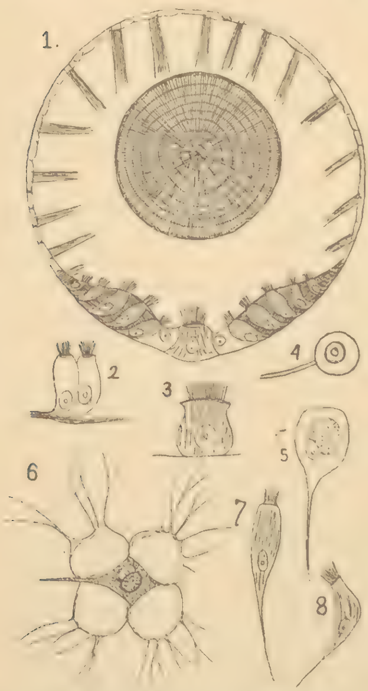

FIG. 10.—Otocyst of Pterotrachea, after Claus: 1, otocyst of P. fredericii, magnified: 2, 7, 8, hearing-cells of the macula; 3, 5, central cell of macula; 6, central cell and four supporting-cells of the macula.

area of its free or inner surface it carries a large number of *Hörhaaren;* viewed from above, the nucleus is seen to lie excentrically, Fig. 10: 5 and 6; the base is prolonged into a tapering process continuous with a nervous fibrilla, Fig. 10: 5. The characters of this cell induce me to regard it as homologous with the bristle-cells outside the *macula.* The central cell is surrounded by four supporting-cells, of the same diameter but less height than itself; they are fastened to the outer membrane by branching processes. Claus affirms that these cells carry no hairs. Ranke says that they do. The four supporting-cells are surrounded by concentric rows of *Hörzellen* (four rows in Pterotrachea fredericii, six or seven in P. coronata and Carinaria). The cells themselves, Fig. 10: 2, 7, 8, are "cylinder cells," swollen in the middle; their bases end each in a tapering process, which bends radially away from the central cell and becomes continuous with a nerve-fibrilla; from the circular central areas of their free surfaces arise the auditory hairs, passing out from the cells through pores of the cuticula; the oval nucleus is placed near the base of the cell; toward the edge of the *macula* the cells gradually grow lower and smaller.

In the dibranchiate Cephalopods the epithelium is reduced to a simple, flat layer, except over the oval *macula acustica* on the upper wall, and over the *crista acustica*, which is a ridge following a curving line on the lower wall. Whether the *crista* is merely the extension of the simple *macula*, or a distinct new structure, is at present impossible to decide, although Grenacher's embryological observations are, if anything, favorable to the latter view. The *ductus Köllikeri* is lined by a ciliated epithelium, the cilia beating toward the main cavity.

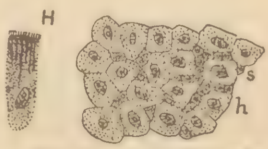

FIG. 11.—Surface view of the epithelium from near the border of the *macula acustica* of Octopus macropus, after Boll: *h*, auditory cell; *s*, indifferent cell; *H*, isolated auditory cell.

The *macula acustica* of Octopus (*Gehörplatte* or *Gehörscheibe*) is covered by high cylinder-cells of two kinds, one having a diameter several times greater than the other (Fig. 11). The small cells are most numerous near the edge of the disc, the centre being composed almost entirely of large cells; these last are stated by Owsjannikow and Kowalewski to be connected each with a nerve-fibrilla, and we

must, therefore, consider them the acoustic cells. When isolated (Fig. 11, *H*), they are seen to have a cylindrical form, with very granular protoplasm, an oval nucleus in their lower part, a fine, cuticular border on their free surfaces, on which rise a large number of very short hairs; in their upper ends are several curious longitudinal streaks in the protoplasm. These streaks are *not* the inward prolongations of the cilia, being much too coarse and also less numerous. The small cells appear to be indifferent, acting only as supports. The *macula* of *Sepia officinalis* contains large cylinder-cells like those of Octopus, but the smaller cells have not yet been observed.

The *crista acustica* is a ridge of sensory cells, supported on either side by several rows of cells, which gradually pass from cylinder-cells into the flat epithelium of the otocyst. In *Octopus* the auditory cells form two rows (Fig. 12), each cell being about as thick as broad; in *Sepia* there is but a single row, and the width or the diameter across the row of each cell is two or three times as great as its breadth, as if the mutual pressure of the cells had flattened them. In general appearance the sensory *crista*-cells resemble the large cells of the *macula* (Fig. 11, *h* and *H*). In Octopus they can be distinctly seen to receive laterally each a nerve-fibrilla (Ows. and K., XX., 31).

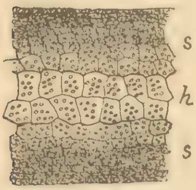

FIG. 12.—Surface view of a small part of the *crista acustica* of Octopus macropus, after Boll: *h*, hearing-cells; *s*, supporting-cells.

The otoliths appear either as numerous small bodies or as a single large one, which, of course, suggests that the large otolith is developed by the agglomeration of several small ones. In fact, certain intermediate stages actually occur, and in the large otoliths of Cephalopods traces of the corresponding small elements have been described.

The small otoliths are found, so far as investigation has yet gone, in most Gasteropods, except Paludina impura, Litorina, etc., in all Pteropods, and in Dentalium and Nautilus. They vary greatly in size, number, and shape. When first formed they are round, but as they enlarge their outline changes. Their most usual final shape is that of a prolate-spheroid, or, in homelier phrase, whetstone-shaped (Fig. 7). Such stones are found in many Gasteropods, in

the Pteropods, and Scaphopods. On the other hand, they may have a distinctly crystalline form, which is stated to agree with that of arragonite. Minute descriptions of the modifications in several species are given by Adolf Schmidt (XXIII.). The fact that of two species of one genus—Paludina—one has multiple, the other a single large otolith, is a forcible argument in favor of the agglomeration of the little to form the large ear-stones.

The large otoliths are found in all Lamellibranchs, in a few Gasteropods, and in all Heteropods and dibranchiate Cephalopods. Except in the Dibranchiata they do not vary greatly from a sphere in shape. They often have a kernel of different appearance from the rest of the stone. They exhibit a radial striation, and often also a system of concentric lines. They sometimes show a cross-shaped figure in their middle. Simroth attributes this appearance to the disposition of the organic matter in the centre. These round otoliths keep up a steady, but not rapid revolution around their own axes. The motive power has yet to be discovered. Those of the dibranchiate Cephalopods are attached by unknown means to the *macula acustica*, and do not revolve. Their shape is also modified; they are pyramidal, with their bases bulging and rounded; the base rests upon the *macula*. In the Decapoda the pyramid is not simple, but has a complicated form, well shown when it is viewed looking down upon it as it rests upon the *macula* (Fig. 13). The otolith is, in proportion to the size of the vesicle, much smaller than in the other mollusca; for example: in Octopus it is only large enough to cover the *macula acustica*.

FIG. 13.—Otolith of Sepia officinalis, after Owsjannikow and Kowalewski.

The otocysts are always filled with fluid, which has never yet been investigated as to its nature.

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